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Comparative demography of six fruit fly (Diptera: Tephritidae) parasitoids (Hymenoptera: Braconidae)

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Abstract

Reproductive and population parameters were calculated for six tephritid fly braconid parasitoids: *Fopius arisanus* (Sonan), *Diachasmimorpha longicaudata* (Ashmead), *Fopius vandenboschi* (Fullaway), *Psyttalia incisi* (Silvestri), *Diachasmimorpha tryoni* (Cameron), and *Psyttalia fletcheri* (Silvestri), reared on a preferred fruit fly host: oriental fruit fly, *Bactrocera dorsalis* (Hendel), Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), or melon fly, *Bactrocera cucurbitae* (Coquillett). Highest numbers of eggs were produced by *F. arisanus*, *D. longicaudata*, and *P. incisi*. Numbers of *P. fletcheri* eggs produced were intermediate and those for *D. tryoni* and *F. vandenboschi* lowest. Intrinsic rates of increase were highest for *F. arisanus* (0.12 per female per day) and *D. longicaudata* (0.12 per female per day) and lowest for *F. vandenboschi* (0.08 per female per day). Highest net reproductive rates were obtained for *P. incisi* (29.4) and lowest for *F. vandenboschi* (10.1). Mean generation times ranged from 27.2 days for *D. longicaudata* to 33.4 days for *P. incisi*. All parasitoid species survived less than 50 days, except *P. incisi* which survived 133 days. Parasitoid species were shorter-lived and possessed lower reproductive rates than their fruit fly counterparts. For example, parasitoid generation times were 24.3%, 26.8%, and 11.7% shorter for *F. arisanus*, *D. tryoni*, and *P. fletcheri* reared on oriental fruit fly, Mediterranean fruit fly, and melon fly, respectively; however, intrinsic rates of increase were 25%, 44%, and 26.6% lower. Implications of these studies are discussed with respect to past and future biological control programs for fruit flies in Hawaii.

Keywords: Braconid parasitoids; Fruit flies; Comparative demography

1. Introduction

Four economically important fruit flies have been introduced accidentally into the Hawaiian Islands. They are melon fly, *Bactrocera cucurbitae* (Coquillett) (introduced in 1895) (Back and Pemberton, 1917); Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (in 1907) (Back and Pemberton, 1918); oriental fruit fly, *B. dorsalis* (Hendel) (in 1945) (van Zwaluwenburg, 1947); and Malaysian fruit fly, *B. latifrons* (Hendel) (in 1983) (Vargas and Nishida, 1985). Establishment of the first three fruit flies was followed by releases of numerous opiine wasps (Gilstrap and Hart, 1987). These releases resulted in many of the most successful examples of classical biological control of fruit flies in the world.

Psyttalia fletcheri (Silvestri), a widespread larval–pupal parasitoid of melon fly in India, was introduced into Hawaii in 1916 (Willard, 1920). Initially, over 50% parasitization of melon fly was reported from collections of infested cucurbits (Willard, 1920). However, later studies revealed that this parasitoid attained high levels of parasitism in fruits of wild *Momordica* sp. but was scarce in cultivated fruits (Nishida, 1953). Following explorations during 1912 and 1913, *Diachasmimorpha tryoni* (Cameron) [= *Opius tryoni* (Cameron)] was introduced into Hawaii from Australia. It displaced *Opius humilis* Silvestri and became the dominant parasitoid on Mediterranean fruit fly (DeBach, 1964). However, coffee

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was the only crop attacked by Mediterranean fruit fly where completely satisfactory biological control occurred (DeBach, 1964).

Although biological control was successful against melon fly and Mediterranean fruit fly, the most notable results were obtained with oriental fruit fly (Clausen et al., 1965). The largest fruit fly program in classical biological control was undertaken to control oriental fruit fly (Purcell, 1998). Bess et al. (1961) listed a total of 32 natural enemies released between 1947 and 1952. *Diachasmimorpha longicaudata* (Ashmead) [= *Opius longicaudatus* (Ashmead)], a parasitoid that attacks second and third instar fruit fly larvae, increased in abundance rapidly in 1948, but was superseded in 1949 by *Fopius vandenboschi* (Fullaway), [= *Opius vandenboschi* Fullaway], which attacks first instar fruit fly larvae. *Fopius vandenboschi* was in turn replaced in 1950 by *Fopius arisanus* (Sonan) [= *Opius oophilus* Fullaway], which attacks eggs and early instar larvae (van den Bosch and Haramoto, 1953). As a result of parasitization (60–79.1%) by *F. arisanus*, the average number of oriental fruit fly larvae per guava (*Psidium guajava* L.) fruit, a major wild reservoir host, declined from 8.5 in 1950 to 2.6 in 1955 (Clausen et al., 1965). Today, *F. arisanus*, *D. longicaudata*, *F. vandenboschi*, and *P. incisi* (Silvestri) are the *most* abundant species attacking oriental fruit fly (Bess et al., 1961; Clausen et al., 1965; Haramoto and Bess, 1970; Nishida, 1953; Stark et al., 1991; Vargas et al., 1993). These species have played a major role in reduction of fruit flies throughout the Hawaiian Islands, particularly in wild host areas. Recent surveys indicate that *F. arisanus* is the primary parasitoid attacking oriental fruit fly and comprises 70–90% of the total parasitoid guild (Purcell et al., 1994; Stark et al., 1991; Vargas et al., 1993; Wong and Ramadan, 1987). Presently, *F. arisanus* is also the major natural enemy of the Mediterranean fruit fly in Hawaii (Vargas et al., 1995).

In the following study, we describe comparative reproduction and demography of *F. arisanus*, *D. longicaudata*, *P. incisi*, *F. vandenboschi*, *D. tryoni*, and *P. fletcheri*. We also compare parasitoid demographic parameters to those for their fruit fly counterparts. Demographic population analysis has diverse applications for examining the dynamics of colonizing or invading species, predicting life history evolution, predicting outbreaks in pest species, and estimating extinction probabilities (McPeek and Kalisz, 1993). This is the first comparative demographic study of Hawaiian fruit fly parasitoids.

2. Materials and methods

Fruit flies and parasitoids were obtained from laboratory colonized stocks maintained at the USDA/ARS, US Pacific Basin Agricultural Research Center in Honolulu, Hawaii. Vargas (1989) has described procedures for rearing fruit flies. Spencer and Mochizuki (1998) and Bautista et al. (1998, 1999, 2000) have described general procedures for rearing fruit fly parasitoids. Laboratory rearing was done in a room maintained at $26 \pm 2\,°C$, $60 \pm 10\%$ relative humidity (RH), and a 10:14 L:D photoperiod.

2.1. Individual adult parasitoid reproductive comparisons

Fopius arisanus parasitoids used in this study were from colonies that were five generations old. *Diachasmimorpha longicaudata*, *P. incisi*, *P. fletcheri*, *D. tryoni*, and *F. vandenboschi* parasitoids used in this study were from colonies that were 45 generations old. At eclosion, 20 pairs of newly emerged adults were placed in separate egging containers (9 cm diameter, 13 cm high). Parasitoids were provided with water and a creamy texture honey (Sioux Honey Association, Sioux City, IA). For the egg–pupal parasitoid, *F. arisanus* eggs were collected by exposing to a paired male and female a slice of papaya fruit (5 cm diameter, 1 cm high) that was initially punctured with 10 holes (2 mm diameter, 2 mm deep, each) and innoculated with 100 oriental fruit fly eggs (Ramadan et al., 1992). *Fopius arisanus* females did not mate in the small cages; therefore, only males were produced. In the case of the larval–pupal parasitoids, host larvae were packed in petri dishes with organdy covers and then exposed to the parasitoids daily for a period of 6 h (Ramadan et al., 1995). Daily mortality of female adults was recorded. Data on oviposition period, fecundity, adult lifespan, and sex ratio were subjected to an analysis of variance and means were separated by a least significant difference test (5% level) (SAS, 1987).

2.2. Egg–pupal parasitoid life tables

Fopius arisanus parasitoids used in this study were from colonies that were 115 generations old. Freshly laid oriental fruit fly eggs were collected for a 1-h period, placed on petri dishes, and exposed for 4–6 h to 50 pairs of *F. arisanus* that had mated inside cubical screen cages (26 cm). A cohort of 100 eggs was selected and placed on 4-cm squares of moist blotting paper. Squares of blotter with eggs were placed inside screen-covered plastic cups that contained 100 g standard wheat diet. Replicate cohorts of eggs and larvae were dissected and examined under a stereomicroscope at 4-day intervals to determine the parasitoid mortality.

Mature larvae were allowed to leave the rearing cups ad libitum into larger plastic cups that contained a layer of 0.5 cm vermiculite, the pupation medium of the fruit fly host. Eight days later, pupae were sifted from the pupation medium and held in plastic cups until eclosion. At eclosion, survivorship of parasitoids was recorded.

Twenty-five pairs of *F. arisanus* adults that had mated inside cubical screen cages (26 cm) were placed inside separate egging containers. Adult parasitoids were provided with water and a creamy texture honey. Parasitoid eggs were collected as described previously. The sex ratio obtained in these studies was 1:1. Daily mortality of female adults was determined.

2.3. Larval–pupal parasitoid life tables

Diachasmimorpha longicaudata, *P. incisi*, *P. fletcheri*, *D. tryoni*, and *F. vandenboschi* parasitoids used in these tests were from colonies that were 190 generations old. For the five species of larval–pupal parasitoids, oriental fruit fly larvae (host for *D. longicaudata*, *F. vandenboschi*, and *P. incisi*), Mediterranean fruit fly larvae (host for *D. tryoni*), or melon fly larvae (host for *P. fletcheri*) packed in modified petri dishes with organdy covers were exposed for 6 h to 200 pairs of *D. longicaudata*, *F. vandenboschi*, *P. incisi*, *D. tryoni*, and *P. fletcheri* (Wong and Ramadan, 1992). Subsequently, a cohort of 100 of these parasitized larvae was placed inside screen-covered plastic cups on the surface of 100 g of the standard wheat diet.

Twenty-five pairs of parasitoids were held in screen cubical cages (26 cm). They were provided with water and honey. Host larvae packed in petri dishes with organdy covers were exposed daily to the parasitoids for 6 h. After oviposition, host larvae were placed in round plastic trays (18 cm diameter, 4 cm h) and provided with fresh larval diet. Trays were held in screen-sided fiberglass boxes ($32 \times 50 \times 15$ cm). One week after exposure to parasitoids, host pupae were sifted from the sand–vermiculite (1:1) pupation medium. Pupae were placed in paper packages and held in emergence cages until adult eclosion. Parasitoid rearing cages were provided with water and honey. Daily mortality of female adults was determined.

The following data were collected: (1) life cycle survivorship and (2) fecundity. Standard life table parameters (Ricklefs, 1990) were calculated from daily records of mortality and fecundity for cohorts of *F. arisanus* (reared on oriental fruit fly), *D. longicaudata* (reared on oriental fruit fly), *F. vandenboschi* (reared on oriental fruit fly), *P. incisi* (reared on oriental fruit fly), *D. tryoni* (reared on Mediterranean fruit fly), and *P. fletcheri* (reared on melon fly) (Carey et al., 1988; Vargas and Carey, 1990; Vargas et al., 1984). Definitions, parameter symbols, and formulae are summarized in Tables 1 and 2. Calculations conform to Carey (1993) and were based on a 1:1 ratio of males:females.

3. Results

3.1. Reproductive parameters for individual parasitoids

Oviposition periods, fecundities, adult lifespans, and sex ratios for *F. arisanus*, *D. longicaudata*, *P. incisi*, *P. fletcheri*, *D. tryoni*, and *F. vandenboschi* were compared (Table 3). Oviposition periods differed significantly for the six species with those for *P. incisi* the longest and *D. tryoni* the shortest. Fecundity differed significantly by species. Highest numbers of eggs were produced by *F. arisanus*, *D. longicaudata*, and *P. incisi*. *Psyttalia fletcheri* numbers were intermediate and those for *D. tryoni* and *F. vandenboschi* lowest. *Psyttalia incisi* had a significantly longer adult lifespan than the other five parasitoid species. Sex ratios did not differ significantly among species.

3.2. Life tables and demographic parameters

Survival, mortality, and fecundity rates for parasitoids reared on oriental fruit fly (*F. arisanus*, *D. longicaudata*, *P. incisi*, and *F. vandenboschi*), Mediterranean fruit fly (*D. tryoni*), and melon fly (*P. fletcheri*) were summarized as life tables. Daily cohort survival (l_x), fecundity (M_x), period mortality (q_x), fraction dying (d_x), and expectation of life (e_x) were calculated (Table 4). Survivorship trends (l_x) for all species were similar (44–50 days), except for the more long-lived *P. incisi* (133 days) (Fig. 1).

Reproductive and population parameters are summarized in Table 5. For the four parasitoids reared on oriental fruit fly, highest gross fecundity rates were obtained for *F. arisanus* (124.9 eggs/female) and lowest for *F. vandenboschi* (34.2 eggs/female). Compared to *F. arisanus*, gross reproductive rates were moderate for the melon fly parasitoid *P. fletcheri* (75.3 eggs/female) and the Mediterranean fruit fly parasitoid *D. tryoni* (54 eggs/female). Numbers of eggs produced per day ranged from 4.2 eggs/day for *F. arisanus* to 1 egg/day for *P. incisi*. Net fecundities for all species ranged from 20.2 to 58.7 eggs per female. Mean age at net fecundity ranged from 27.5 to 30.9 days. Intrinsic rates of increase were highest for *F. arisanus* (0.12 per female per day) and *D. longicaudata* (0.12 per female per day) and lowest for *F. vandenboschi* (0.08 per female per day). Highest net reproductive rates were obtained for *P. incisi* (29.4 per generation) and lowest for *B. vandenboschi* (10.1). Mean generation times ranged from 27.2 days for *D. longicaudata* to 33.4 days for *P. incisi*.

4. Discussion

Observations during the 1950s suggested that dominance and displacement of parasitoids introduced into Hawaii for control of oriental fruit fly were related to how early in the fruit fly life cycle the parasitoid attacked (van den Bosch and Haramoto, 1953). Initially, *D. longicaudata*, a late larval parasitoid, was the dominant species only to be replaced by *F. vandenboschi*, an early larval parasitoid, which in turn was displaced by *F. arisanus*, an egg–larval parasitoid DeBach (1964). More recent surveys by Wong and Ramadan (1987) and Vargas et al. (1993) have indicated abundance of

Table 1
Definitions and formulae for various life table and demographic parameters

Parameter	Definition	Formula
x	Age interval in days	
l_x	Proportion of females surviving to start of the age interval	
m_x	Number of female eggs laid by average female at age x	
M_x	Average number of offspring produced by female at age x	
Preoviposition period	Amount of time prior to eggs being laid	
Gross fecundity rate	Theoretical natality rate during lifetime of organism	$\sum_{x=\alpha}^{\beta} M_x$
Net fecundity rate	Total number of fertile eggs laid by female during her lifetime	$\sum_{x=\alpha}^{\beta} l_x M_x$
Daily reproduction	Average number of eggs produced per day in terms of entire female lifespan	$\sum_{x=\alpha}^{\beta} M_x/(\omega - \varepsilon)$
Net reproductive rate (R_0)	Per generation contribution of newborn females to the next generation	$\sum_{x=\alpha}^{\beta} l_x m_x$
Intrinsic rate of increase (r)	Rate of natural increase in a closed population	$1 = \sum_{x=\alpha}^{\beta} e^{-rx} l_x m_x$
Finite rate of increase (λ)	Factor by which a population increases in size from time t to time $t+1$	e^r
Intrinsic birth rate (b)	The per capita instantaneous rate of birth in the stable population	$1/\sum_{x=1}^{\omega} e^{-rx} l_x$
Intrinsic death rate (d)	The per capita instantaneous rate of death in the stable population	$b - r$
Mean generation time (T)	The time required for a newborn female to replace herself R_0-fold	$(\log_e R_0)/r$
Doubling time (DT)	The time required for the population to increase twofold	$(\log_e 2)/r$

Adopted from Carey (1993).

Table 2
Insect life table parameters

Parameter	Notation	Formula	Units
Survival rates			
Cohort survival	l_x	$\prod_{y=0}^{\omega} p_y$	Proportion
Expectation of life at age x	e_x	$\sum_{x=y}^{\omega} l_y/l_x$	Days
Mortality rates			
Fraction dying at age x	d_x	$l_x - l_{x+1}$	Proportion
Period mortality	q_x	d_x/l_x	Proportion

Adopted from Carey (1993).

Table 3
Oviposition period, fecundity, adult lifespan, and sex ratio for *F. arisanus* (*F.a.*), *D. longicaudata* (*D.l.*), *P. incisi* (*P.i.*), *P. fletcheri* (*P.f.*), *D. tryoni* (*D.t.*), and *F. vandenboschi* (*F.v.*)

Species	Oviposition period (d)	Fecundity (eggs per female)	Lifespan (d)	Sex ratio (proportion female)
	(Mean ± SEM)			
F.a.	11.00 ± 1.78b	119.40 ± 24.71a	17.30 ± 3.89b	—
D.l.	9.33 ± 1.34bc	93.00 ± 3.88ab	15.67 ± 4.10b	0.59 ± 0.05a
P.i.	16.50 ± 2.08a	90.90 ± 12.98ab	36.60 ± 3.89a	0.49 ± 0.10a
P.f.	8.80 ± 0.81bc	69.30 ± 11.21cb	13.40 ± 3.89b	0.64 ± 0.05a
D.t.	6.60 ± 0.78c	50.40 ± 6.67c	13.40 ± 3.89b	0.55 ± 0.06a
F.v.	11.00 ± 1.50b	33.38 ± 5.92c	22.00 ± 4.35b	0.57 ± 0.08a

Values in each column followed by the same letter are not significantly different at the $P = 0.05$ level (Proc GLM, LSD Test, SAS, 1989).

oriental fruit fly parasitoids in the order *F. arisanus* > *D. longicaudata* > *P. incisi* > *F. vandenboschi*. It is recognized that laboratory-reared insects were used in this study and that some aspects of the ecology and genetics of laboratory insects may differ from their wild counterparts. With that caveat in mind, certain broad characteristics with respect to life history and colonization traits of parasitoids are evident from our demographic data. In addition to the effects of competition, host stage, and fruit type suggested by other studies (Bess et al., 1961; Haramoto and Bess, 1970; van den Bosch and Haramoto, 1953), our demographic data suggest that the present abundance pattern for fruit fly parasitoids in Hawaii may also be influenced by the dominance of species with high intrinsic rates of increase. For example, *F. arisanus* and *D. longicaudata*, with high intrinsic rates of increase (0.12 per female per day), are among the most abundant parasitoids attacking oriental fruit fly (Stark et al., 1991; Vargas et al., 1993; Wong and Ramadan, 1987). *F. vandenboschi*, on the other hand, with a comparatively low intrinsic rate of increase (0.08 females per female), is relatively rare (Ramadan et al., 1995). Not surprisingly, when two species with high intrinsic rates of increase are present (*F. arisanus* and

Table 4
Life tables (x, age in days; l_x, cohort survival; M_x, average number of offspring; q_x, period mortality; d_x, fraction dying at age x; e_x, expectation of life) for *F. arisanus*, *D. longicaudata*, *P. incisi*, *F. vandenboschi*, *D. tryoni*, and *P. fletcheri*

Age (x)	l_x	M_x	q_x	d_x	e_x
F. arisanus (reared on oriental fruit fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	26.05
2	0.98	0.00	0.02	0.02	25.56
3	0.96	0.00	0.03	0.03	25.07
4	0.93	0.00	0.02	0.02	24.85
5	0.91	0.00	0.02	0.02	24.37
6	0.89	0.00	0.02	0.02	23.90
7	0.87	0.00	0.02	0.02	23.43
8	0.85	0.00	0.02	0.02	22.95
9	0.83	0.00	0.01	0.01	22.48
10	0.82	0.00	0.02	0.02	21.74
11	0.80	0.00	0.03	0.02	21.26
12	0.78	0.00	0.03	0.02	20.78
13	0.76	0.00	0.03	0.02	20.30
14	0.74	0.00	0.01	0.01	19.82
15	0.73	0.00	0.03	0.02	19.08
16	0.71	0.00	0.01	0.01	18.59
17	0.70	0.00	0.03	0.02	17.84
18	0.68	0.00	0.03	0.02	17.34
19	0.66	0.00	0.02	0.01	16.83
20	0.65	0.00	0.02	0.01	16.08
21	0.64	0.00	0.00	0.00	15.31
22	0.64	3.92	0.02	0.01	14.31
23	0.63	6.32	0.00	0.00	13.52
24	0.63	11.46	0.02	0.01	12.52
25	0.62	9.35	0.00	0.00	11.71
26	0.62	6.19	0.02	0.01	10.71
27	0.61	4.29	0.05	0.03	9.87
28	0.58	5.45	0.03	0.02	9.33
29	0.56	10.00	0.04	0.02	8.63
30	0.54	7.84	0.09	0.05	7.91
31	0.49	5.14	0.06	0.03	7.61
32	0.46	7.15	0.04	0.02	7.04
33	0.44	4.80	0.16	0.07	6.32
34	0.37	5.10	0.11	0.04	6.32
35	0.33	2.42	0.06	0.02	5.97
36	0.31	0.22	0.29	0.09	5.29
37	0.22	4.62	0.09	0.02	6.05
38	0.20	2.75	0.10	0.02	5.55
39	0.18	6.91	0.17	0.03	5.06
40	0.15	4.11	0.13	0.02	4.87
41	0.13	4.88	0.15	0.02	4.46
42	0.11	3.71	0.18	0.02	4.09
43	0.09	5.50	0.11	0.01	3.78
44	0.08	0.00	0.25	0.02	3.13
45	0.06	0.00	0.33	0.02	2.83
46	0.04	2.75	0.25	0.01	2.75
47	0.03	0.00	0.33	0.01	2.33
48	0.02	0.00	0.50	0.01	2.00
49	0.01	0.00	0.00	0.00	2.00
50	0.01	0.00	1.00	0.01	1.00
D. longicaudata (reared on oriental fruit fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	26.26
2	0.98	0.00	0.02	0.02	25.78
3	0.96	0.00	0.03	0.03	25.29
4	0.93	0.00	0.02	0.02	25.08
5	0.91	0.00	0.02	0.02	24.60
6	0.89	0.00	0.02	0.02	24.13
7	0.87	0.00	0.02	0.02	23.67
8	0.85	0.00	0.02	0.02	23.20
9	0.83	0.00	0.01	0.01	22.73
10	0.82	0.00	0.02	0.02	22.00
11	0.80	0.00	0.03	0.02	21.53
12	0.78	0.00	0.03	0.02	21.05
13	0.76	0.00	0.03	0.02	20.58
14	0.74	0.00	0.01	0.01	20.11
15	0.73	0.00	0.03	0.02	19.37
16	0.71	0.00	0.01	0.01	18.89
17	0.70	0.00	0.03	0.02	18.14
18	0.68	0.00	0.03	0.02	17.65
19	0.66	0.00	0.02	0.01	17.15
20	0.65	0.00	0.02	0.01	16.40
21	0.64	0.00	0.00	0.00	15.64
22	0.64	1.33	0.02	0.01	14.64
23	0.63	1.00	0.02	0.01	13.86
24	0.62	0.56	0.00	0.00	13.06
25	0.62	1.22	0.02	0.01	12.06
26	0.61	29.00	0.00	0.00	11.25
27	0.61	29.00	0.02	0.01	10.25
28	0.60	8.67	0.00	0.00	9.40
29	0.60	7.11	0.02	0.01	8.40
30	0.59	4.78	0.02	0.01	7.53
31	0.58	5.44	0.00	0.00	6.64
32	0.58	1.63	0.12	0.07	5.64
33	0.51	2.57	0.06	0.03	5.27
34	0.48	0.71	0.04	0.02	4.54
35	0.46	0.00	0.15	0.07	3.70
36	0.39	0.17	0.33	0.13	3.18
37	0.26	0.75	0.23	0.06	3.27
38	0.20	0.00	0.35	0.07	2.95
39	0.13	0.00	0.31	0.04	3.00
40	0.09	0.00	0.22	0.02	2.89
41	0.07	0.00	0.43	0.03	2.43
42	0.04	0.00	0.25	0.01	2.50
43	0.03	3.00	0.33	0.01	2.00
44	0.02	1.00	0.50	0.01	1.50
45	0.01	0.01	1.00	0.01	1.00
P. incisi (reared on oriental fruit fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	36.43
2	0.98	0.00	0.02	0.02	36.15
3	0.96	0.00	0.03	0.03	35.89
4	0.93	0.00	0.02	0.02	36.01
5	0.91	0.00	0.02	0.02	35.78
6	0.89	0.00	0.02	0.02	35.56
7	0.87	0.00	0.02	0.02	35.36
8	0.85	0.00	0.02	0.02	35.16
9	0.83	0.00	0.01	0.01	34.99
10	0.82	0.00	0.02	0.02	34.40
11	0.80	0.00	0.03	0.02	34.24
12	0.78	0.00	0.03	0.02	34.09
13	0.76	0.00	0.03	0.02	33.96
14	0.74	0.00	0.01	0.01	33.85
15	0.73	0.00	0.03	0.02	33.30
16	0.71	0.00	0.01	0.01	33.21
17	0.70	0.00	0.03	0.02	32.67
18	0.68	0.00	0.03	0.02	32.60
19	0.66	0.00	0.02	0.01	32.56
20	0.65	0.00	0.00	0.00	32.05
21	0.65	0.00	0.00	0.00	31.05
22	0.65	0.00	0.00	0.00	30.05
23	0.65	0.00	0.02	0.01	29.05

Table 4 (*continued*)

Age (x)	l_x	M_x	q_x	d_x	e_x
24	0.64	0.00	0.00	0.00	28.48
25	0.64	0.00	0.00	0.00	27.48
26	0.64	0.29	0.00	0.00	26.48
27	0.64	4.50	0.00	0.00	25.48
28	0.64	3.68	0.00	0.00	24.48
29	0.64	7.75	0.00	0.00	23.48
30	0.64	6.93	0.02	0.01	22.48
31	0.63	3.64	0.00	0.00	21.83
32	0.63	7.32	0.00	0.00	20.83
33	0.63	9.96	0.00	0.00	19.83
34	0.63	10.71	0.00	0.00	18.83
35	0.63	5.25	0.00	0.00	17.83
36	0.63	5.67	0.02	0.01	16.83
37	0.62	1.52	0.02	0.01	16.08
38	0.61	4.27	0.03	0.02	15.33
39	0.59	5.58	0.05	0.03	14.81
40	0.56	4.15	0.04	0.02	14.55
41	0.54	7.00	0.13	0.07	14.06
42	0.47	1.90	0.04	0.02	15.00
43	0.45	0.00	0.02	0.01	14.62
44	0.44	2.16	0.02	0.01	13.93
45	0.43	0.00	0.23	0.10	13.23
46	0.33	0.71	0.12	0.04	15.94
47	0.29	2.71	0.10	0.03	17.00
48	0.26	0.00	0.08	0.02	17.85
49	0.24	0.00	0.08	0.02	18.25
50	0.22	0.33	0.09	0.02	18.82
51	0.20	0.88	0.25	0.05	19.60
52	0.15	0.00	0.07	0.01	24.80
53	0.14	0.00	0.07	0.01	25.50
54	0.13	0.60	0.00	0.00	26.38
55	0.13	1.80	0.00	0.00	25.38
56	0.13	0.00	0.08	0.01	24.38
57	0.12	1.40	0.00	0.00	25.33
58	0.12	0.00	0.00	0.00	24.33
59	0.12	0.00	0.00	0.00	23.33
60	0.12	0.20	0.08	0.01	22.33
61	0.11	0.00	0.00	0.00	23.27
62	0.11	0.20	0.00	0.00	22.27
63	0.11	0.00	0.00	0.00	21.27
64	0.11	0.20	0.00	0.00	20.27
65	0.11	0.00	0.09	0.01	19.27
66	0.10	0.00	0.20	0.02	20.10
67	0.08	0.00	0.00	0.00	23.87
68	0.08	0.67	0.13	0.01	22.87
69	0.07	0.00	0.00	0.00	25.00
70	0.07	0.67	0.00	0.00	24.00
71	0.07	2.67	0.00	0.00	23.00
72	0.07	0.00	0.14	0.01	22.00
73	0.06	0.00	0.00	0.00	24.50
74	0.06	0.00	0.00	0.00	23.50
75	0.06	1.33	0.00	0.00	22.50
76	0.06	1.67	0.00	0.00	21.50
77	0.06	0.00	0.17	0.01	20.50
78	0.05	0.00	0.00	0.00	23.40
79	0.05	0.00	0.20	0.01	22.40
80	0.04	0.00	0.00	0.00	26.75
81	0.04	0.00	0.00	0.00	25.75
82	0.04	0.50	0.25	0.01	24.75
83	0.03	0.00	0.00	0.00	31.67
84	0.03	0.00	0.00	0.00	30.67
85	0.03	0.00	0.00	0.00	29.67
86	0.03	0.00	0.00	0.00	28.67
87	0.03	0.00	0.00	0.00	27.67

Table 4 (*continued*)

88	0.03	0.00	0.00	0.00	26.67
89	0.03	0.00	0.00	0.00	25.67
90	0.03	0.00	0.00	0.00	24.67
91	0.03	0.00	0.00	0.00	23.67
92	0.03	0.00	0.00	0.00	22.67
93	0.03	0.00	0.33	0.01	21.67
94	0.02	0.00	0.00	0.00	31.00
95	0.02	0.00	0.00	0.00	30.00
96	0.02	0.00	0.00	0.00	29.00
97	0.02	0.00	0.00	0.00	28.00
98	0.02	0.00	0.00	0.00	27.00
99	0.02	0.00	0.00	0.00	26.00
100	0.02	0.00	0.00	0.00	25.00
101	0.02	0.00	0.00	0.00	24.00
102	0.02	0.00	0.00	0.00	23.00
103	0.02	0.00	0.00	0.00	22.00
104	0.02	0.00	0.00	0.00	21.00
105	0.02	0.00	0.00	0.00	20.00
106	0.02	0.00	0.00	0.00	19.00
107	0.02	0.00	0.00	0.00	18.00
108	0.02	0.00	0.00	0.00	17.00
109	0.02	0.00	0.00	0.00	16.00
110	0.02	0.00	0.00	0.00	15.00
111	0.02	0.00	0.00	0.00	14.00
112	0.02	0.00	0.00	0.00	13.00
113	0.02	0.00	0.00	0.00	12.00
114	0.02	0.00	0.00	0.00	11.00
115	0.02	0.00	0.50	0.01	10.00
116	0.01	0.00	0.00	0.00	18.00
117	0.01	0.00	0.00	0.00	17.00
118	0.01	0.00	0.00	0.00	16.00
119	0.01	0.00	0.00	0.00	15.00
120	0.01	0.00	0.00	0.00	14.00
121	0.01	0.00	0.00	0.00	13.00
122	0.01	0.00	0.00	0.00	12.00
123	0.01	0.00	0.00	0.00	11.00
124	0.01	0.00	0.00	0.00	10.00
125	0.01	0.00	0.00	0.00	9.00
126	0.01	0.00	0.00	0.00	8.00
127	0.01	0.00	0.00	0.00	7.00
128	0.01	0.00	0.00	0.00	6.00
129	0.01	0.00	0.00	0.00	5.00
130	0.01	0.00	0.00	0.00	4.00
131	0.01	0.00	0.00	0.00	3.00
132	0.01	0.00	0.00	0.00	2.00
133	0.01	0.00	1.00	0.01	1.00
F. vandenboschi (reared on oriental fruit fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	30.15
2	0.98	0.00	0.02	0.02	29.74
3	0.96	0.00	0.03	0.03	29.34
4	0.93	0.00	0.02	0.02	29.26
5	0.91	0.00	0.02	0.02	28.88
6	0.89	0.00	0.02	0.02	28.51
7	0.87	0.00	0.02	0.02	28.14
8	0.85	0.00	0.02	0.02	27.78
9	0.83	0.00	0.01	0.01	27.42
10	0.82	0.00	0.02	0.02	26.74
11	0.80	0.00	0.03	0.02	26.39
12	0.78	0.00	0.03	0.02	26.04
13	0.76	0.00	0.03	0.02	25.70
14	0.74	0.00	0.01	0.01	25.36
15	0.73	0.00	0.03	0.02	24.70
16	0.71	0.00	0.01	0.01	24.37
17	0.70	0.00	0.03	0.02	23.70

Table 4 (*continued*)

Age (x)	l_x	M_x	q_x	d_x	e_x
18	0.68	0.00	0.03	0.02	23.37
19	0.66	0.00	0.02	0.01	23.05
20	0.65	0.00	0.00	0.00	22.38
21	0.65	0.00	0.02	0.01	21.38
22	0.64	0.00	0.00	0.00	20.70
23	0.64	0.00	0.02	0.01	19.70
24	0.63	0.00	0.00	0.00	19.00
25	0.63	0.75	0.02	0.01	18.00
26	0.62	1.38	0.00	0.00	17.27
27	0.62	4.38	0.02	0.01	16.27
28	0.61	6.13	0.00	0.00	15.52
29	0.61	5.38	0.00	0.00	14.52
30	0.61	3.38	0.02	0.01	13.52
31	0.60	0.88	0.00	0.00	12.73
32	0.60	0.63	0.02	0.01	11.73
33	0.59	2.00	0.00	0.00	10.92
34	0.59	0.88	0.02	0.01	9.92
35	0.58	1.13	0.00	0.00	9.07
36	0.58	1.50	0.00	0.00	8.07
37	0.58	0.00	0.02	0.01	7.07
38	0.57	2.50	0.00	0.00	6.18
39	0.57	1.14	0.14	0.08	5.18
40	0.49	0.00	0.06	0.03	4.86
41	0.46	0.00	0.07	0.03	4.11
42	0.43	1.33	0.05	0.02	3.33
43	0.41	0.80	0.61	0.25	2.44
44	0.16	0.00	0.19	0.03	3.69
45	0.13	0.00	0.15	0.02	3.31
46	0.11	0.00	0.09	0.01	2.73
47	0.10	0.00	0.20	0.02	1.90
48	0.08	0.00	0.88	0.07	1.13
49	0.01	0.00	1.00	0.01	1.00
D. tryoni (reared on Mediterranean fruit fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	26.23
2	0.98	0.00	0.02	0.02	25.74
3	0.96	0.00	0.03	0.03	25.26
4	0.93	0.00	0.02	0.02	25.04
5	0.91	0.00	0.02	0.02	24.57
6	0.89	0.00	0.02	0.02	24.10
7	0.87	0.00	0.02	0.02	23.63
8	0.85	0.00	0.02	0.02	23.16
9	0.83	0.00	0.01	0.01	22.70
10	0.82	0.00	0.02	0.02	21.96
11	0.80	0.00	0.03	0.02	21.49
12	0.78	0.00	0.03	0.02	21.01
13	0.76	0.00	0.03	0.02	20.54
14	0.74	0.00	0.01	0.01	20.07
15	0.73	0.00	0.03	0.02	19.33
16	0.71	0.00	0.01	0.01	18.85
17	0.70	0.00	0.03	0.02	18.10
18	0.68	0.00	0.03	0.02	17.60
19	0.66	0.00	0.02	0.01	17.11
20	0.65	0.00	0.00	0.00	16.35
21	0.65	0.00	0.02	0.01	15.35
22	0.64	0.00	0.00	0.00	14.58
23	0.64	0.00	0.00	0.00	13.58
24	0.64	0.00	0.00	0.00	12.58
25	0.64	0.00	0.02	0.01	11.58
26	0.63	19.93	0.00	0.00	10.75
27	0.63	11.86	0.00	0.00	9.75
28	0.63	1.22	0.02	0.01	8.75
29	0.62	5.96	0.02	0.01	7.87
30	0.61	6.15	0.00	0.00	6.98
31	0.61	0.69	0.07	0.04	5.98
32	0.57	3.08	0.05	0.03	5.33
33	0.54	2.57	0.04	0.02	4.57
34	0.52	1.50	0.17	0.09	3.71
35	0.43	0.33	0.33	0.14	3.28
36	0.29	0.08	0.34	0.10	3.38
37	0.19	0.25	0.37	0.07	3.63
38	0.12	0.00	0.42	0.05	4.17
39	0.07	0.00	0.14	0.01	5.43
40	0.06	0.00	0.17	0.01	5.17
41	0.05	0.33	0.00	0.00	5.00
42	0.05	0.00	0.20	0.01	4.00
43	0.04	0.00	0.00	0.00	3.75
44	0.04	0.00	0.25	0.01	2.75
45	0.03	0.00	0.00	0.00	2.33
46	0.03	0.00	0.67	0.02	1.33
47	0.01	0.00	1.00	0.01	1.00
P. fletcheri (reared on melon fly)					
0	1.00	0.00	—	—	—
1	1.00	0.00	0.02	0.02	25.85
2	0.98	0.00	0.02	0.02	25.36
3	0.96	0.00	0.03	0.03	24.86
4	0.93	0.00	0.02	0.02	24.63
5	0.91	0.00	0.02	0.02	24.15
6	0.89	0.00	0.02	0.02	23.67
7	0.87	0.00	0.02	0.02	23.20
8	0.85	0.00	0.02	0.02	22.72
9	0.83	0.00	0.01	0.01	22.24
10	0.82	0.00	0.02	0.02	21.50
11	0.80	0.00	0.03	0.02	21.01
12	0.78	0.00	0.03	0.02	20.53
13	0.76	0.00	0.03	0.02	20.04
14	0.74	0.00	0.01	0.01	19.55
15	0.73	0.00	0.03	0.02	18.81
16	0.71	0.00	0.01	0.01	18.31
17	0.70	0.00	0.03	0.02	17.56
18	0.68	0.00	0.03	0.02	17.04
19	0.66	0.00	0.02	0.01	16.53
20	0.65	0.00	0.00	0.00	15.77
21	0.65	0.00	0.00	0.00	14.77
22	0.65	0.00	0.00	0.00	13.77
23	0.65	1.97	0.02	0.01	12.77
24	0.64	2.15	0.00	0.00	11.95
25	0.64	4.03	0.00	0.00	10.95
26	0.64	10.93	0.00	0.00	9.95
27	0.64	4.66	0.00	0.00	8.95
28	0.64	7.90	0.02	0.01	7.95
29	0.63	9.40	0.02	0.01	7.06
30	0.62	7.22	0.03	0.02	6.16
31	0.60	6.29	0.03	0.02	5.33
32	0.58	5.12	0.07	0.04	4.48
33	0.54	5.06	0.33	0.18	3.74
34	0.36	3.16	0.11	0.04	4.11
35	0.32	3.76	0.22	0.07	3.50
36	0.25	1.62	0.16	0.04	3.20
37	0.21	0.35	0.52	0.11	2.62
38	0.10	0.21	0.30	0.30	3.40
39	0.07	0.33	0.14	0.01	3.43
40	0.06	1.17	0.17	0.01	2.83
41	0.05	0.00	0.40	0.02	2.20
42	0.03	0.00	0.33	0.01	2.00
43	0.02	0.00	0.50	0.01	1.50
44	0.01	0.00	1.00	0.01	1.00

D. longicaudata), the species attacking the host first (eggs near the fruit surface) will be more abundant than the one attacking the host later (larvae dispersed in the fruit). Also, in large fruits such as guava, the eggs are more vulnerable than the larvae. *F. arisanus* possesses two important traits: early attack and a high intrinsic rate of increase. Consequently, numbers of *F. arisanus* often comprise greater than 90% of the braconid guild parasitizing oriental fruit fly in guava (Vargas et al., 1993). There is mounting evidence to suggest that *F. arisanus* is also the dominant natural enemy of Mediterranean fruit fly (Vargas et al., 1995), displacing other larval parasitoids such as *D. longicaudata* and *D. tryoni*.

Future classical biological control for fruit flies in Hawaii should consider a high intrinsic rate of increase as a desirable trait in exploring for new parasites that would have maximum impact on the target pest species. Although *F. arisanus* parasitization of oriental fruit fly is cited as the best example of biological control of fruit flies (Waterhouse, 1993), melon fly, a severe economic pest of vegetables throughout Hawaii, has few effective natural enemies. Only *P. fletcheri* has proven moderately effective in Hawaii. In the present study, although *P. fletcheri* possessed a relatively high intrinsic rate of increase ($r = 0.11$) that approached that of *F. arisanus* ($r = 0.12$), its fecundity was found to be significantly

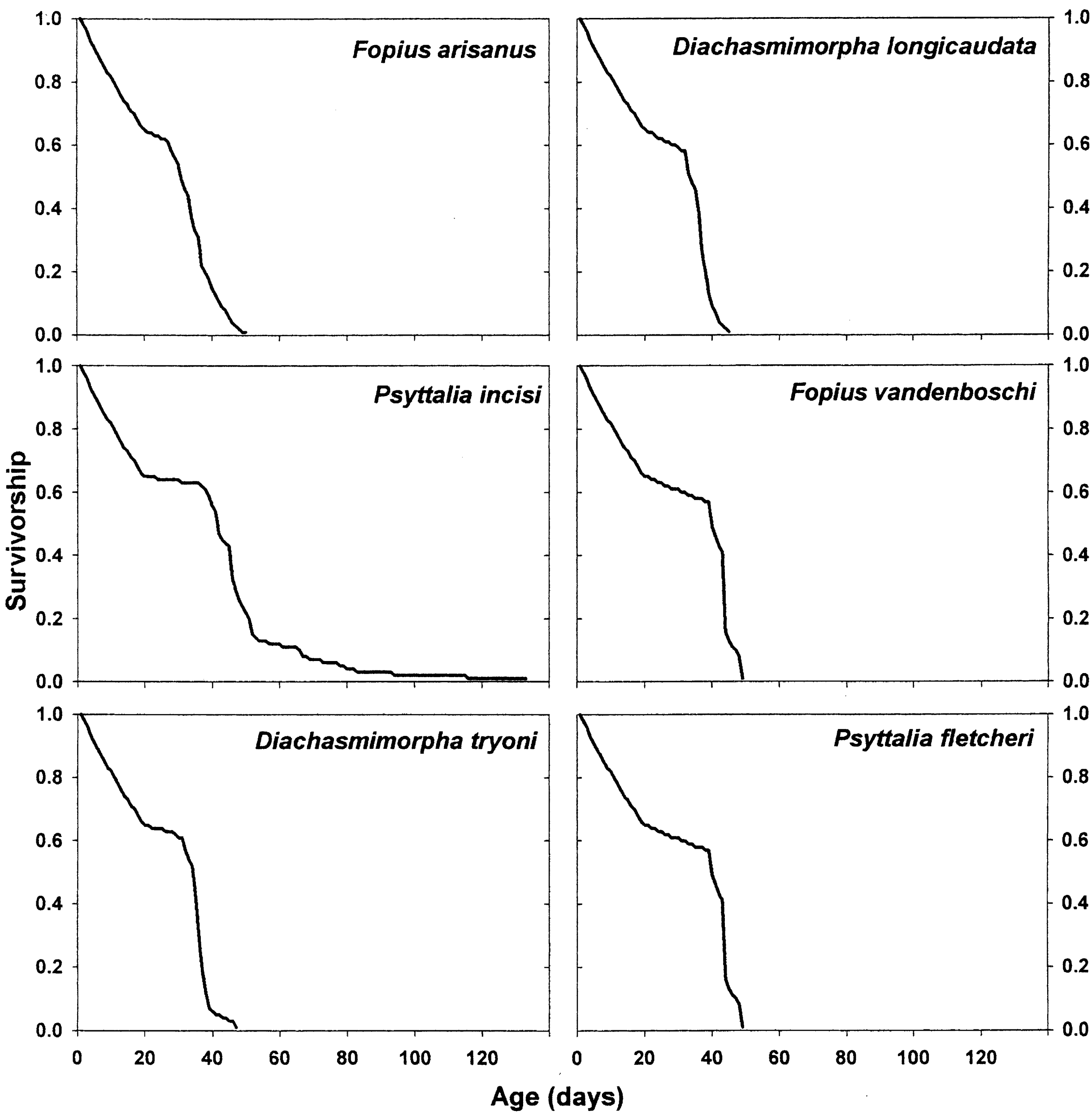

Fig. 1. Survivorship (l_x) curves for all stages of *Fopius arisanus*, *Diachasmimorpha longicaudata*, *Psyttalia incisi*, *Fopius vandenboschi*, *Diachasmimorpha tryoni*, and *Psyttalia fletcheri*.

Table 5
Reproductive and population parameters for six parasitoid species: *F. arisanus* (*F.a.*), *D. longicaudata* (*D.l.*), *P. incisi* (*P.i.*), *F. vandenboschi* (*F.v.*), *D. tryoni* (*D.t.*), and *P. fletcheri* (*P.f.*)

	Species					
	F.a.	*D.l.*	*P.i.*	*F.v.*	*D.t.*	*P.f.*
Reproductive parameters						
Gross fecundity (eggs/female)	124.9	97.9	108.8	34.2	54.0	75.3
Net fecundity (eggs/female)	54.7	56.4	58.7	20.2	32.8	43.1
Eggs per day (eggs/day)	4.2	3.9	1.0	1.3	2.4	3.3
Eggs per insect-day (eggs/day)	3.6	3.6	2.1	1.1	2.8	3.1
Mean age gross fecundity (days)	31.5	28.2	38.4	31.3	28.2	29.5
Mean age net fecundity (days)	28.6	27.5	34.8	30.9	28.0	28.8
Population parameters						
Intrinsic rate of increase ($1/t$)	0.12	0.12	0.10	0.08	0.10	0.11
Finite rate of increase (per day)	1.13	1.13	1.12	1.08	1.11	1.11
Intrinsic birth rate ($1/t$)	0.15	0.15	0.13	0.10	0.13	0.14
Intrinsic death rate ($1/t$)	0.03	0.03	0.03	0.02	0.03	0.03
Net reproductive rate (per gen)	27.4	28.2	29.4	10.1	16.4	21.5
Mean generation time (days)	27.3	27.2	33.4	30.3	27.8	28.3

lower. Furthermore, *P. fletcheri's* effectiveness has been limited by other factors such as low abundance and patchy distribution of preferred wild cucurbit hosts, utilization of the late larval–pupal fruit fly host stages, and heavy use of insecticides in cultivated truck crop areas (Harris et al., 1986; Nishida, 1953; Vargas et al., 1990). Greater reductions in melon fly populations might be obtained through the importation and establishment of new natural enemies with high intrinsic rates of increase and an earlier stage of parasitization that complements the larval–pupal parasitoid *P. fletcheri*.

Significant advances in mass rearing methods have made possible field testing of large-scale releases of parasites for control of fruit flies (Bautista et al., 1999, 2000; Purcell, 1998). This includes all six species of parasitoids included in the present study. Knipling (1995) has discussed the theoretical potential for augmentative release of opiine parasitoids for suppression of fruit fly populations. Several augmentative releases of fruit fly parasites have indicated the potential for suppression of fruit flies. In Hawaii, augmentative releases of *D. tryoni* over a 13 km^2 area showed that overall parasitism rates were increased by 48% (Wong et al., 1991; Wong et al., 1992). In Florida, mass releases of *D. longicaudata* over suburban areas (5 and 14 km^2) reduced *Anastrepha suspensa* (Loew), Caribbean fruit fly, populations by 95% (Sivinski et al., 1996). Although augmentative releases of fruit fly parasitoids have been proposed and tested many times, field survival, adaption to different ecological habitats, and colonization of parasitoids after release are poorly understood. Our demographic data are useful in the construction of basic parasite/pest population growth and survival models that identify the most promising species. Comparative data are useful in selecting parasitoid species for rapid colonization and high survival in the field. Models based on survivorship and fecundity, when validated in the field, will be useful for predicting population trends and making pest management decisions with respect to increasing the effectiveness of parasites on pest populations.

Demographic studies for fruit fly parasitoids have been limited to studies by Carey et al. (1988) for *P. incisi* and those by Bautista et al. (1998) for *F. arisanus*. Parameters obtained in the present study for *P. incisi* and *F. arisanus* were similar. Many previous demographic studies under similar laboratory conditions have examined survival and reproduction of economically important fruit flies in Hawaii (Vargas and Carey, 1990; Vargas et al., 1984). Mediterranean fruit fly with the shortest mean generation time ($T = 31.5$ days) and the second highest net reproductive rate ($R_0 = 317.5$) possessed the highest intrinsic rate of increase ($r = 0.18$). Oriental fruit fly with the highest R_0 (418.5) but a longer generation time ($T = 37.3$ days) possessed the second highest r (0.16). Melon fly with a comparatively low R_0 (255.4) and a long generation time ($T = 37.3$ days) had the lowest r (0.15). Clearly based on the present study, parasitoids had shorter generation times and lower rates of increase than their fruit fly host counterparts. For example, although parasitoid generation times were 24.3%, 26.8%, and 11.7% shorter for *F. arisanus*, *D. tryoni*, and *P. fletcheri* reared on oriental fruit fly, Mediterranean fruit fly, and melon fly, respectively; intrinsic rates of increase were 25%, 44%, and 26.6% lower. These findings suggest that augmentative mass releases of parasites as a stand-alone technology may not be sufficient to bring about economic suppression of a species and adjunct mortality agents may be required for significant reduction of the pest population. Because of the high economic and environmental costs for eradication of fruit flies in Hawaii, control efforts are now shifting towards areawide integrated pest management of fruit flies. For example, the integration of sterile insect technique (Wong et al., 1992), a pesticide-laced protein bait (Vargas et al., 2001), or male annihilation (Vargas et al., 2000) with parasitoids may lower reproductive rates of pest fruit flies and enhance the effectiveness of parasitoids.

In conclusion, previous biological control life table analyses have focused on the impact of the natural enemy on the host as a mortality factor (Bellows and Van Driesche, 1999). The present study differs by focusing primarily on the natural enemy. Simple life table and demographic models were constructed for comparison of six species of parasitoids introduced into Hawaii for biological control of fruit flies. These models provide an ecological framework for future biological control programs in Hawaii.

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